The Neo-Riparian butterfly fauna of western Argentina

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Abstract. In the arid and semiarid zones of western Argentina (San Juan, Mendoza and Neuquén Provinces), establishment and naturalization of exotic Salicaceae (willows and poplars) over the past 200 years has created a new type of mesic environment ("Neo-Riparian") which in turn has acquired a distinctive butterfly fauna derived from the regional species pool. These species are nearly all multivoltine and feed on naturalized exotic (weedy) host-plants. These phenomena are compared to the urban-suburban butterfly faunas of California, USA.

Resumen. En las zonas áridas o semiáridas del occidente argentino, en las provincias de San Juan, Mendoza y Neuquén, la introducción, cultivación y naturalización de Salicáceas exóticas (Álamos y Sauces) a partir de 1808 ha ocasionado un nuevo biotopo ("Neo-Ribereño") con una fauna correspondiente de mariposas, derivadas de la fauna regional. Son casi todas multivoltinas y utilizan plantas-hospederas naturalizadas, mayormente malezas (yuyos). Se compara estos fenómenos con sus pares en las faunas urbanas/suburbanas de mariposas californianas (EE.UU.).

Key words: poplars, willows, introduced species, exotic weeds, host plants.

Introduction

Sometimes the iconic landscape of a geographic region is not "natural," but the product of human activity. Sometimes that landscape is dominated by a single species of non-native plant. For many people, Blue Gum (*Eucalyptus globulus*) is virtually synonymous with lowland California—but it has been present there for only a little more than a century (Groenendaal, 1983). For many—visitors and natives alike—Lombardy Poplar (*Populus nigra italica*) is similarly iconic of lowland Argentina, including much of Patagonia. In semiarid and arid parts of Argentina the most conspicuous trees – and often the only trees—are members of the family Salicaceae, Poplars (genus *Populus*) and Willows (genus *Salix*). But there is only one native member of the family, *Salix humboldtiana*, in the Argentine flora. All the other Poplars and Willows one sees there are introduced from the Northern Hemisphere. Some have naturalized.

Shapiro (1984) compared the Patagonian butterfly fauna with those of the arid and semiarid American West. He noted that in North America butterfly diversity is characteristically higher in riparian than in steppe or shrubsteppe habitats, while in Patagonia the reverse is true. The proximate cause of this disparity is the adaptive radiation and speciation of the Patagonian Pronophilini (Nymphalidae, Satyrinae), which are grass feeders; there is no parallel in the North American fauna. However, this comparison only took account of the faunas associated with native vegetation and autochthonous plant communities. The present-day visitor to northern Patagonia or to irrigated valleys in the Monte, the high desert of west-central Argentina (regionally known as the Cuyo), encounters many more butterflies in riparian zones than elsewhere. This is true not only of numbers of individuals, but of taxonomic and visual diversity as well (the Pronophilines are monotonously brown): the number of species is small, but they represent a variety of lineages. This fauna as a unit appears to be of recent origin, recruited from the geographically proximate species pool. I call it the "Neo-Riparian" Fauna insofar as there does not appear to have been a significant native riparian fauna. This paper describes its ecology, makeup, and probable history. It is based on 31 years of travel and field work in Argentina, as well as on the Argentine literature.

Received: 21 July 2008
Accepted: 9 August 2008

Background of the Neo-Riparian Community

Shapiro (1991) summarizes Argentine phytogeography to that time, relying heavily on the work of Cabrera (1971). Cabrera divides the country into two Regions, only one of which, the Neotropical, concerns us here. It is subdivided into three domains. The Monte belongs to the Chaco Domain. Precipitation varies from 80-250 mm (locally higher), mean temperature from 13-17.5C, with strong E-W and N-S climatic gradients. There is year-round

precipitation, with the heaviest falling in summer thunderstorms of monsoonal character. As usual in monsoonal climates, there is great interyear variability, and droughts and floods are both frequent. The vegetation is diverse, but dominated throughout by creosotebush (*Larrea*) and mesquite (*Prosopis*). The Monte corresponds to the Sonoran Desert of North America, to which it has been compared ecologically in great detail (Orians & Solbrig, 1977). The region is well-watered by major rivers descending from the Andes, flush with snowmelt in spring and early summer and often fed by glacial meltwater. These waters have been harnessed for both agriculture and urban use, especially for the important viticultural industry. The Payunia district in SW Mendoza Province forms an ecotone to the Western District of northern Patagonia, which Cabrera classifies in the Andean-Patagonian Domain based on floristic differences. It is a narrow fringe of shrub-steppe containing a mix of bunchgrasses and such shrubs as *Mulinum, Trevoa, Colliguaya* and *Nassauvia.* Mean annual temperature at Chos Malal in the N is 13.4°C. Precipitation ranges from 100-270 mm over the Patagonian steppe, heaviest in the W, and is more heavily frontal as one travels closer to the source of subantarctic air masses. Farther S and E is the Central District, containing the most arid part of Patagonia, from the center of the Province of Rio Negro through the province of Santa Cruz. Winters are long with frequent frost and snow, but the proximity of the ocean keeps winter minima mostly above -10°C. Summers are cool, rather cloudy and windy. Again, irrigation water is relatively abundant from Andean sources. Fruit crops and alfalfa are widely grown.

In pre-European times the extent of riparian woodland in western Argentina was very limited. The principal species were Mesquites (*Prosopis flexuosa, P. chilensis*) and Maitén (*Maytenus boaria*). The only native willow is *Salix humboldtiana.* The shrub *Baccharis salicifolia* and perennial herb *Pluchea* (*Tessaria*) *dodoneaefolia* were common. Although the latter two are excellent nectar sources for butterflies, these communities do not appear to have a distinctive butterfly fauna, as riparian communities commonly do in the western United States. Species diversity is inevitably higher in the adjacent and much more extensive shrub-steppe and matorral communities, where many species of Satyrinae routinely occur. Intact examples of natural riparian vegetation are encountered mainly in the Andean foothills today; virtually all floodplain areas in the Cuyo have been transformed by human intervention.

The basic reference for historical ecology in Argentina is *Memoria Verde* by Antonio Elio Brailovsky and Dina Foguelman (2006). This is a comprehensive historical overview of human impacts on the Argentine landscape and environment, from precolonial times to the present. With 716 footnotes, it serves as the port of entry to a rich, if little-known (outside Argentina) literature. Very briefly, Brailovsky and Foguelman tell how the agriculturalization of the country in the 19th Century led to the removal of the narrow fringe of native riparian vegetation: "Then there appeared a new factor precipitating erosion: agriculture, realized by temporary leaseholders whose interest in preserving the nearby soil was zero, and whose agronomic knowledge was initially sparse. They had to use all the land and the firewood available. Thus they cut down all the trees, including those that protected the margins of watercourses, which when the rains and floods came ended up carrying the fertility of the nearby soils far, far away." This formed part of a general pattern of wasteful agricultural practices that lasted into the 20th Century (Zarrilli, 2001). In 1886 Florentino Ameghino, an Argentine original—an autodidact-polymath best remembered as a paleontologist who developed the rich fossil beds of Patagonia and flew off on flights of patriotic fancy, declaring Patagonia the cradle of humankind—published a monograph, "Droughts and floods in the province of Buenos Aires," which is still reckoned a classic of its kind. In it he developed a detailed plan for water management, including "...the creation of artificial forests and the obligatory forestation of the margins of water courses [which] will delay erosion and permit the maintenance of the soil as a renewable resource."

Ameghino's proposals were poorly implemented systematically at a regional level, although the Immigration and Colonization Law of 1879 offered cash prizes for every 1000 trees planted on private property. Other legislation made transfer of title from the state to pioneering settlers conditional on the planting of at least 200 trees. The Mendoza Provincial Law of 1897 (Law 39) again rewarded those who planted trees, and in 1907 Mendoza institutionalized Arbor Day (Law 384). Meanwhile, construction of the national railway system had led to a demand for both ties and fuelwood that in turn led to further deforestation, mainly in the north of the country. However, the impacts were felt in the semiarid west; Ameghino wrote that in the provinces of San Juan and Mendoza "instead of augmenting them, they are destroying the few groves there had been." And flooding and alluvial deposits increased downstream in consequence. Ameghino argued that planned forestation offered multiple benefits: beyond its use in flood control, it offered shade for livestock,

recuperation of exhausted soils, and windbreaks for the protection of orchards and crops. For those who took this work seriously, the question became "What species to plant." The answer was already at hand.

The introduction of poplars in western Argentina dates from 1808 when the Spanish colonist Juan Cobo imported from Cadiz, via Chile, saplings of Lombardy Poplar and Black Poplar (*Populus nigra*) as well as other exotic trees to plant on his property in Mendoza. They thrived and grew so rapidly that they were soon propagated vegetatively and dispersed throughout the region, obviating the need to import expensive lumber for construction from Chile, Paraguay or Tucumán. The value of this introduction was so apparent that after the liberation from Spanish rule in 1810, Cobo was granted honorary Argentine citizenship for his service to the economy. This was a singular honor, since loyal Spaniards were widely discriminated against and were often the victims of harassment or violence. As early as the 1830s poplars were being used as windbreaks to shelter orchards and vineyards from both desiccation and frost. They spread to other parts of the country and were eagerly adopted, but by the 1930s disease problems in the more humid regions led to the introduction of new species, varieties and hybrids (some sterile, and only propagated vegetatively) from Italy, Germany and the United States. These eventually found their way to the Cuyo and northern Patagonia, where they "took off." Calderón (2006) writes "Here begins what can be called the second stage of poplar cultivation in our region; the new varieties grow faster and give better lumber...than our characteristic 'Creole poplars.' Still, one can yet contemplate beautiful rows of these magnificent trees in some streets of our oases..."

According to the National Poplar Commission (Comisión Nacional del Álamo, 2004) some 110,000 hectares of Argentine territory are devoted to cultivation of exotic willows and poplars. The three regions most active in the industry are the Paraná Delta north of Buenos Aires (where willows predominate) and the humid pampa of the central and northern parts of the province of Buenos Aires and the south of Santa Fe; the irrigated Cuyo in Mendoza and San Juan; and the upper valley of the Río Negro in northern Patagonia (where both genera are widely grown, but poplars are more widespread) Achinelli (2006) gives an excellent overview of the industry as it now exists.

In the Cuyo and northwestern Patagonia today, in the Provinces of San Juan, Mendoza and Neuquén, bottomlands near towns almost inevitably are planted in Salicaceae or present a vegetation dominated by naturalized Salicaceae, commonly interdigitated with small cultivated farm and garden plots and supporting small numbers of horses, mules and other grazing domestic animals. As noted at the beginning of this article, this is today a very characteristic Argentine landscape, even though the vegetation is largely non-native. From an ecological perspective it represents a repeating community type, which has selected a distinctive butterfly fauna from the regional species pool. Butterflies are characteristically much more abundant in this "Neo-Riparian" setting than in the adjacent more-or-less natural steppe; the species mix is very different; and most of the species are today breeding on naturalized exotic host plants, which is not the case in steppe.

In addition to willows and poplars representing a number of introductions (species, varieties and hybrids), the Neo-Riparian vegetation routinely includes other exotic trees including Boxelder (*Acer negundo*), Red Mulberry (*Morus rubra*), Blue Gum (*Eucalyptus globulus* and others), Black Locust (*Robinia pseudoacacia*), Siberian Elm (*Ulmus sibirica*),and occasionally Ash species (*Fraxinus*), fruit trees, and others. The following is a partial list of plants commonly encountered in the understory of Neo-Riparian forest. The vast majority are naturalized exotic weeds, and many are of cosmopolitan distribution. Most are familiar weeds in temperate North America as well.

APIACEAE: *Conium maculatum, Foeniculum vulgare.* ASTERACEAE: *Acroptilon* (*Centaurea*) *repens, Carduus nutans, Carduus pycnocephalus, Centaurea solstitialis, C. cyanus, Cichorium intybus, Cirsium vulgare, Matricaria chamomilla, Onopordon acanthium.* BORAGINACEAE: *Echium vulgare.* BRASSICACEAE: *Cardaria draba, Diplotaxis tenuifolia, Eruca sativa, Hirschfeldia incana, Raphanus sativus, Sisymbrium orientale.* CARYOPHYLLACEAE: *Saponaria officinalis.* CHENOPODIACEAE: *Atriplex hastata, Atriplex patula, Kochia scoparia.* CONVOLVULACEAE: *Convolvulus arvensis.* FABACEAE: *Galega officinalis, Medicago sativa.* MALVACEAE: *Malva neglecta.* POACEAE: *Cynodon dactylon.*

The butterfly fauna

In addition to the species enumerated here, species from the adjacent shrubsteppe may enter Neo-Riparian areas, particularly in search of nectar. Since the reverse movement does not occur, this merely enhances the apparent diversity. All host records given here are based on direct observation of oviposition and/or larval feeding in the Neo-Riparian community since 1977. I have visited more than 30 Neo-Riparian areas in San Juan, Mendoza and Neuquén, some on

multiple occasions.

Family PIERIDAE

Tatochila mercedis vanvolxemii Capronnier. (Common name "Lechera troyana")
Common; multivoltine, seasonally polyphenic. Males patrol along the edges of windbreaks and hedgerows; females found mostly in open successional fields. Populations to the east (e.g., Las Lajas, Neuquén) are apparently "pure" *vanvolxemii*, but those at the base of the Andes, such as at Barreal and Calingasta, San Juan, often show some degree of introgression from the Mediterranean Chilean subspecies *T. m. mercedis* Esch. (see Shapiro, 1991a, pp.156-166). All the known host plants in the Neo-Riparian are exotic: BRASSICACEAE: *Cardaria draba, Diplotaxis tenuifolia, Eruca sativa, Hirschfeldia incana, Lepidium perfoliatum, Raphanus sativus, Sisymbrium orientale.* The range of this entity encompasses the Monte, much of the Pampa, and the warmest parts of the eastern Patagonian steppe. In most of this region it has no native Brassicaceous hosts and may originally have been confined to Capparidaceae in the arid and subarid west; much of its current range, which extends to metropolitan Buenos Aires, may be an opportunistic response to Brassicaceous weed introductions.

Tatochila autodice Hubner. (Common name "Lechera común")
Common, multivoltine. This species consistently occurs in partially shaded, cooler and more humid microhabitats than the preceding, but they can be found together along roadsides and windbreaks. The southernmost populations, e.g. at Chos Malal, Neuquén, show slight phenotypic tendencies toward the Chilean-Patagonian subspecies *T. a. blanchardi* Butler, with which it intergrades in western Patagonia (Shapiro, 1986).
Again, all the known hosts here are exotic, though further south in the ecotone between the Patagonian steppe and Andean forest it breeds on native Tropaeolaceae. BRASSICACEAE: *Cardaria draba, Eruca sativa, Hirschfeldia incana, Raphanus sativus.*

Colias vauthierii Guerin. (Apparently no common name)
Common from Chos Malal and Las Lajas south, with two to three generations per year. A species of cool, moist vegas and mallines, this butterfly extends north through the province of Mendoza in the Andes but has not been found in the Neo-Riparian in Mendoza or San Juan. It is extremely abundant at Las Lajas. Females are highly variable, but always white. This species never feeds on Alfalfa (*Medicago sativa*), though it may nectar on it. The only recorded hosts in the Neo-Riparian are FABACEAE: *Trifolium repeus* (and probably other clovers).

Colias lesbia Fabricius. (Common name "Oruga de la alfalfa", "Isoca de la alfalfa")
Common to seasonally abundant in the north (Mendoza and San Juan) and occasional to common in the south (Neuquén), breeding on Alfalfa (*Medicago sativa*) even in the smallest patches. About half of the females are white; cold-season individuals are small, with narrowed black borders above and more or less gray shading on the hindwing beneath. At least three generations/year. This species may not overwinter in the SW portion of its range, often not being seen until the second brood in January.

Family NYMPHALIDAE

Auca coctei Guerin. (Common name "Mariposa negra común")
The only Pronophiline Satyr associated consistently with Neo-Riparian habitats, this species is common in Neuquen province but has not been found in Mendoza or San Juan. At Las Lajas it is abundant in dappled light and shade and even in dense shade, preferentially visiting the yellow flowers of native *Senecio*, but also introduced weeds. It has been collected in January and February and may be univoltine. It is a grass feeder, but its host in the Neo-Riparian has not been determined.

Vanessa carye Hubner. (Common names "Mariposa colorada," "Dama cuatro ojos," "Dama manchada," "Pirpinto manchado")
Common throughout, with multiple generations. Males are conspicuously territorial in late afternoon, often in front of poplar windbreaks with a westerly or northwesterly exposure. Both sexes often visit the native *Baccharis* and *Pluchea* and introduced species of thistles and knapweeds. MALVACEAE: *Malva neglecta* (*M. parviflora*) and native species of *Sida.* URTICACEAE: *Urtica urens.*

Agraulis vanillae Linnaeus. (Common names "Mariposa de manchas plateadas," "Espejitos," "Mariposa de espejos," "Nacarada")
Common in the north (Mendoza, San Juan) and variably present in Neuquén, depending on the presence of host plants, which are cultivated and non-native in the region. Multiple-brooded, flying all year except in the coldest weather. Hosts: PASSIFLORACEAE: *Passiflora species.*

Figure 1. Views of Neo-Riparian habitats in western Argentina. All pictures by AMS.

Upper left: Lombardy Poplar windbreak in Barreal, San Juan; the arid shrubsteppe is visible at the horizon.
Upper right: Spontaneous vegetation of naturalized riparian trees, including Black Locust, Willow, and two species of Poplars. Drying Poison Hemlock in foreground. Arid shrubsteppe visible in distance. Las Lajas, Neuquén.
Center left: Orchards with Lombardy Poplar windbreak and dense population of Yellow Star Thistle in foreground. Las Lajas, Neuquén.
Center right: Spontaneous riparian vegetation including large Weeping Willow. Bachelor's-Button blooming in foreground. Las Lajas, Neuquén.
Lower left: View inside a Lombardy Poplar hybrid clone plantation, Chos Malal, Neuquén, showing mesic conditions. Across the road from this site was arid shrubsteppe with no green visible.
Lower right: Proliferation of weedy Brassicaceae along a farm road; *Tatochila mercedis vanvolxemii* abundant and *T. autodice* common; male *T. vanvolxemii* patrol along the edge of the poplar windbreaks. Malargüe, Mendoza.

Family RIODINIDAE

Aricoris signata Stichel. (Common name "Colage común")
This small, inconspicuous Metalmark is common in the Neo-Riparian community in Mendoza and San Juan but has not been found in Neuquén. It visits Alfalfa flowers and sits with the wings spread. It is apparently multivoltine. The recorded host elsewhere is the native vetch *Vicia graminea*; the host in the Neo-Riparian has not been determined.

Family HESPERIIDAE

Erynnis funeralis Scudder & Burgess. (Common name "Saltarín fúnebre" or "Hesperia negra")
Very common throughout, multivoltine. Commonly visiting Alfalfa, thistle and various Composite flowers and often entering shade. Despite numerous citations of Alfalfa as a larval host, no such relationship has been observed in the Neo-Riparian, where its sole observed host is FABACEAE: *Robinia pseudoacacia* (Shapiro, 2008). Eggs are laid mostly on coppice and sucker growth.

Pyrgus americanus bellatrix Plötz. (Common Name "Cuadriculada americana")
Common and multivoltine throughout. Adults fly along linear habitats, visiting Alfalfa and numerous other flowers and also (males) mud puddles. Host: MALVACEAE: *Malva neglecta.*

Hylephila zapala Evans.
This little-known species is fairly common at Malargue (Mza.) and Chos Malal and Zapala (Neuquén) in association with its native host plant, the turfgrass *Distichlis spicata.* At least two, probably three broods. Visits Yellow Star Thistle (*Centaurea solstitialis*) and Alfalfa flowers. Males perch on grass or bare soil.

Hylephila phyleus Drury. (Common Name "Saltarín leonado," "Saltarín dorado"—this name is also used for *Polites vibex catilina* Plötz, not in the Neo-Riparian fauna)
Abundant in Mendoza and San Juan; occasional in western Neuquén. Multivoltine. The highly territorial males perch high on roadside weeds, and both sexes eagerly visit Alfalfa, thistles and other flowers. The only host so far observed is introduced Bermuda Grass, *Cynodon dactylon.*

Hylephila signata Blanchard.
Common in Neo-Riparian habitat in Neuquén, but not observed further north. At least two broods. Often visits Clover flowers (*Trifolium species*); perches on or near the ground. Host plant presumably a grass, but undetermined locally.

Lerodea eufala Edwards. (Common Name "Saltarín semicírculo")
Common to occasionally abundant in the second half of the season, January through March or April, in Mendoza and San Juan; unrecorded in Neuquén. Rarely encountered in spring. Flies low and appears non-territorial; often along ditches; often found nectaring on Alfalfa with *Hylephila phyleus* and *Erynnis funeralis.* Host not determined in the Neo-Riparian.

This is a small fauna, only 14 species in total, forming a reproducible association in a well-defined anthropogenic habitat type. It is, moreover, structured geographically: *Colias vauthierii*, *Auca coctei* and *Hylephila signata* are essentially Patagonian and do not extend into Mendoza, while *Aricoris signata*, *Hylephila phyleus*, and *Lerodea eufala* are essentially northern and do not extend into Neuquén. Since all of these occurrences are in isolated floodplain or irrigated oases in the high desert and the distances among them are similar, the limitations would appear to be climatic. *Colias lesbia* and perhaps *Agraulis vanillae* show very dynamic ranges, expanding and contracting seasonally and perhaps overwintering only sporadically in areas with harsher winters, much as *Colias eurytheme* and *A. vanillae* do in the United States.

All the species except possibly *Auca coctei* are multivoltine. Of the 10 species whose Neo-Riparian host plants are known, all but one (*Hylephila zapala*) feed on non-native hosts and one (*Agraulis vanillae*) is entirely dependent on cultivated hosts. (Use of non-native hosts by native butterflies in the Southern Cone of South America has been observed at low altitudes in mid-latitudes (Shapiro, 1991a), in the high Andes (Shapiro, 2006) and in the Subantarctic (Shapiro, 1991b).) These characteristics are strikingly similar to those of the urban/suburban lowland butterfly fauna of northern California as described by Shapiro(2002) and Graves and Shapiro (2003). In fact, despite the enormous distances involved, the northern California weedy butterfly fauna shares four species with the Neo-Riparian: *Agraulis vanillae*, *Erynnis funeralis*, *Hylephila phyleus* and *Lerodea eufala. Vanessa carye* is the sister-species of the North American *V. annabella*; the two are extremely similar and only recently diverged (Shapiro & Geiger, 1989). *Hylephila phyleus* is the only member of its (largely Andean) genus in the Nearctic and might be introduced there. *Erynnis funeralis* is the only member of its Holarctic (mostly Nearctic) genus in South America and could also be an introduction.

As Graves and Shapiro (2003) argued, the availability of weedy hosts has probably facilitated large-scale butterfly range changes in historic time, such that species able to make use of them now occupy both areas and habitats previously closed to them.

In both lowland northern California and the Argentine Neo-Riparian community, the creation of local mesic conditions has permitted the establishment of both exotic host plants and butterflies able to exploit them. The stark contrasts between a Neo-Riparian bottomland, lush and green, and the high desert or shrubsteppe often directly across the road, underscore the impact human activity has had on the butterfly fauna of western Argentina.

Acknowledgements

I particularly thank Germán San Blas, Ana Soledad Sallenave and Marcelo Tognelli for help and companionship, the Instituto Argentino de Investigaciones de Zonas Áridas (Mendoza) for providing a base of operations, and Argentino/as too numerous to list for their cordial hospitality over the past 31 years.

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